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Palynology of *Berberis* (Berberidaceae)

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Abstract

Pollen morphological observations were made from oil emmersion light microsopy and scanning electron microscopy for 21 species of *Berberis* in relation to palynodiversity within the genus. No palynological relationship between the different sections is encountered. Pollen morphological subdivision of the genus is proposed and a palynological key to different species is provided for species identification based on pollen characters. Based on apertual evolution within the genus, phylogeny of the genus is traced and it is found that the apertural evolution is monophyletic originating from inaperturate (*B. macrosepala*) and basic 3-colpate forms to the advanced spiraperturate pollen of (*B. asiatica*). The taxa *B. lycium* represent the intermediate form or a "connecting link" in the chain of pollen evolution. The evolution of surface ornamentation within the taxa is also parallel to the aperture evolution.

INTRODUCTION

The exine of pollen is endowed with such stable morphological characters which are genetically fixed and do not get influenced by the environmental fluctuations. These characters are specific for different genera and may vary from species to species. Pollen morphology has therefore been recognised as a dependable tool for tackling taxonomic problems and for elucidating systematic relationships, phylogeny and evolution of related plant groups. Among the bases of angiosperm phylogeny, pollen morphology is unique in that through no other study can one obtain as great an amount of information from so little material within a short time (Walker and Doyle, 1975). Principal pollen morphological characters which are phylogenetically useful have been extensively applied in making comparisons and interpretations of relationships and evolutionary trends in higher plants.

Berberis pollen has been poorly known to date. Barring a few examples of species worked out by Kumazawa (1936), Nair (1965) and Nowicke and Skvarla (1981) the majority of the species remain palynologically underexplored. Lund (1935) described *B. dictyophylla*, Kumazawa (1936) described pollen of Berberidaceae in general, Erdtman (1952) stated that *Berberis* pollen are generally spiraperturate and similar to *Mahonia* pollen. Nair (1965) described 5 species of *Berberis* namely *B. aristata, B. asiatica, B. lycium, B. umbellata* and *B. vulgaris*. He stated that the spiraperturate condition is formed by the union of 3-4 colpi.

In view of above, an investigation on pollen morphology of Indian species of *Berberis* was undertaken to develop a comprehensive idea on taxonomy, phylogeny, affinity and diversity of different species of the taxon. The main objectives are : (1) to determine the extent of pollen diversity within the genus, (2) to provide a species identification key for the taxon, (3) to determine phylogenetic relationships, if any, within the taxon, (4) to determine the extent of palynological relationship between different sections (Ahrendt) of the genus and (5) to provide pollen morphological subdivisions of the genus. In addition to this, the analysis would offer a good opportunity to evaluate the hypothesis of Spiraperturate pollen types being derived from the 3-poly (-syn-) colpate type.

CONSTRAINTS IN THE STUDY

The genus *Berberis* L. (Berberidaceae) which consists of about 55 species in India is confined to the high terrains in the Himalayan mountains. Almost all species have a different phenological behaviour. It is therefore, an extremely difficult task to collect the flower buds in different flowering seasons for palynogical studies. Besides, the Berberidaceae collections in Indian herbaria are also very poor (see Rao *et. al.*, 1994 for details) and the difficulty in procuring the flower buds from these collections is further enhanced as the collections are often in fruiting stage.

MATERIAL AND METHODS

The polliniferous material used in this study was mainly obtained from the herbarium specimens of LWG. Some Fresh material in form of mature flower buds was also procured through the courtesy of members of the Berberidaceae survey teams of NBRI to the Himalaya. In some cases the available material was very little (just one bud or a single anther). In such cases unacetolysed SEM photographs have been used. A list of the material used in the study, including their accession numbers, is given in Table 1.

In all, 32 samples of *Berberis* under 21 species representing almost every section except Heteropadae and Ulicinae have been studied for their pollen morphology. The method used for light microscope study (LM) was acetolysis (Erdtman 1960). Only mature flower buds and flowers were used as a source of pollen.

The acetolysed pollen were divided into two parts. One part was used for making permanent pollen slide preparations for LM, while the other part was used for scanning electron microscopy (SEM). Pollen for LM was transferred in glycerine jelly on microslides, evenly spread and sealed with a cover glass.

For SEM, the acetolysed pollen was dehydrated and mounted on a brass stub on which a piece of cover glass was prefixed (for pollen preparation with single anthers the pollen was not acetolysed, instead, the anther was dehydrated and gently squeezed on the stub). The pollen were

Table 1. Details of material used in the study

S.No.	Taxa	Collector's Name	Coll. No.	Herbaria
1.	*B. apiculata*	S.I.	224	CAL
2.	*B. aristata*	M.A. Rao	15676	BSD
3a.	*B. asiatica* var. *asiatica*	A.K Goel	65807	BSD
b.		K.C. Sahni	5187	DD
4.	*B. chitria* var. *chitria*	A.K. Saklani	212386	LWG
5.	*B. chitria* var. *occidentalis*	B.N. Mehrotra	66	LWG
6.	*B. coriaria* var. *coriaria*	T. Husain & T.S. Rana	210333	LWG
7.	*B. coriaria* var. *patuls*	B. Datt & B. Lal	212275	LWG
8.	*B. dasyclada*	Kingdom-Ward	13700	BM
9.	*B. griffithiana* var. *griffithiana*	T.S. Rana & Party	210220	LWG
10.	*B. griffithiana* var. *pallida*	Ludlow. Sheriff & Taylor	3097	BM
11.	*B. hamiltoniana*	N.C. Nair	22386	BSD
12.	*B. incrassata*	T.S. Rana & B. Datt	210334	LWG
13.	*B. insignis* var. *insignis*	A.K. Goel	14236	LWG
14.	*B. insignis* var. *shergaonensis*	Kingdom-Ward	13617	BM
15.	*B. jaeschkeana* var. *jaeschkena*	B.D. Naithani	14236	LWG
16.	*B. jaeschkeana* var. *usteriana*	R.N. Parker	2078	DD
17.	*B. jaeschkeana* var. *bimblica*	B.S. Aswal	10064	LWG
18.	*B. kashmiriana*	Ludlow	122	BM
19.	*B. koeheneana*	Parker	2047	DD
20.	*B. kunawurensis* var. *kunawurensis*	U.C. Bhattacharya	51878	BSD
21.	*B. lycium* var. *lycium*	Ram Lakhan	9818	LWG
22.	*B. lycium* var. *subfascicularis*	B. Datt & B. Lal	212229	LWG
23.	*B. lycium* var. *simlensis*	K.K. Singh & Party	3417	LWG
24.	*B. lycium* var. *subvirescens*	B. Datt & B. Lal	210588	LWG
25.	*B. marcosepala* var. *macrosepala*	Smith & Cove	1492	CAL
26.	*B. marcosepala* var. *sakdenensis*	D.C.S. Raju & B. Mitra	7427	BSHC
27.	*B. pachyacantha* var. *pachyacantha*	U.C. Bhattacharya	45911	BSD
28.	*B. petiolaris* var. *garhwalana*	B. Datta & B. Lal	212280	LWG
29.	*B. petiolaris* var. *extensa*	Polunin, Sykes & Williams	2066	BM
30.	*B. praecipua*	Ludlow, Sheriff & Hicks	16015	BM
31.	*B. replicata* var. *dispar*	T.S. Rana & Pary	210335	LWG
32.	*B. sanei*	Mehrotra & Party	2439	LWG

coated with a thin film of gold (about 200 A) under sputter coater JFC-1100. The specimens were observed in JEOL-JSM 35 C SEM at an accelerating voltage of 10 kv. The pollen measurements were made under LM at magnification of 100 X in cedar wood oil emersion medium using occular micrometer placed in the eyepiece and calibrated with the stage micrometer. The following parameters were measured according to Erdtman (1969) - polar axis (P), equatorial exis (E), pollen diameter, exine thickness including both ectoexine and endoexine layers, aperture width (in case of broad apertures), poral diameter and endopore diam. The quotient P/E was determined. All measurements were taken for 25-30 grains and average calculated.

Detailed surface ornamentation was observed both under LM and SEM. Pollen shape was determined as visualised under SEM. The pollen morphological descriptions were based on observation of the entire palynocontent of the slide under LM and stub under SEM. SEM photographs were taken for the best chosen grains clearly showing the key characters.

The apertural condition is described on the basis of apertural uniformity in >60% grains of each sample. Due to the highly variable nature of the spiral apertures the terms "spiroid" and "colpoid" are used to designate apertures which are intermediate to perfectly spirapaturate and perfectly polycolpate types respectively (Erdtman, 1952).

The terminology used for pollen morphological characters is based on that given by Erdtman *et. al.* (1960) and modified by Nair (1970) with some more modifications to express the apertural details. Morphological characterisation covers the five groups of characters namely aperture (primary), exine ornamentation (secondary), exine strata, size and shape (tertiary). Any other feature of importance in taxonomic identification has also been mentioned.

RESULTS

The pollen morphology of Indian *Berberis* is highly variable (Table 2). The apertural condition ranges from inaperturate, 3-4 poly/syn-colpate, semi-spiraperturate to spiraperturate. In some cases pores are also found in association with colpi or spiral. The aperture membrane is generally smooth or granular. Surface ornamentation varies from psilate-smooth, psilate-rough, punctate, fossulate-foveolate and warted types; pollen size ranges from 23 μm to 70 μm with spheroidal, prolate-spheroidal, to prolate grains. The exine strata is homogenous (not clearly differentiated into foot layer collumella and tectum); exine thickness ranges from 1.5 to 4 μm at mesapertural zone reaching upto 6 μm at aperture margins. A margo (thickened aperture margin) is occasionally present, and is often represented by a region bordering the aperture over which exine sculpturing may not extend.

In view of such vast heterogeneity of pollen characters a general description does not suffice for all the species of this taxon. Therefore, a detailed pollen morphological description for each species and variety has been provided (species arranged alphabeatically in pollen description). A pollen identification key is also provided for an easy identification of the different species.

Palynology of *Berberis*

KEY TO SPECIES OF *BERBERIS* POLLEN

1. Pollen spiraperturate; spiral variable.

2. Spiral simple, single, regularly coils round the grain winding parallely to delineate the surface into a perfect continuous strip ..... *B. asiatica*

2. Spiral forms a complex; may be continuous or broken into short spirals branched or unbranched, irregularly curved, undulating or self winding.

3. Branched or bifurcated spirals with curved, coalescing branches.

3. Unbranched, continuous or interrupted spirals, self-winding or undulating in 'U' or 'S' manner, encircling the entire grain.

4. Pollen surface delimited into two-three elongated, tightly interlocking pieces; exine surface foveolate-fossulate with dense punctae ..... *B. chitria*

4. Pollen surface delimited into four - six angular, rounded or irregular plates.

5. Exine surface psilate-rough; grains spheroidal ..... *B. coriaria*

5. Exine surface minutely punctate; grains prolate ..... *B. apiculata*

6. Pore also present; pollen diam 23 μm ..... *B. hamiltoniana*

6. Pore absent; pollen diam equal to or > 30 μm.

7. Pollen surface with perforrations (punctae)

8. Grains spheroidal ..... *B. pachyacantha*

8. Grains prolate-spheroidal to subprolate

9. Surface roughly punctate or foveolate-fossulate ..... *B. jaeschkeana*

9. Surface smoothly punctate

10. Punctae sparse, slightly elongated ..... *B. dasyclada*

10. Punctae ill-defined, rounded, densely spread ..... *B. incrassata*

7. Pollen surface without perforrations

11. Roughly warted / in raised lumps

12. Grains prolate in shape ..... *B. kashmiriana*

12. Grains spheroidal in shape ..... *B. griffithiana*

11. Foveolate, grains spheroidal to sub-prolate ..... *B. lycium*

B. aristata DC. (Figs. 3-4)

Grains 3-colpate; colpi zonal or irregular, of different size, often colpus very large covering the entire grain, membrane smooth, tips acute, margin thickened uniformly; aperture sunken with raised margins folded over the colpus, 6-9 μm wide. Exine 6 μm thick at aperture margin and 3 μm at intercolpi-region; ectoexine thicker than endoexine surface psilate, smooth; columella indistinct. Grains irregularly shaped due to folded apertural margins; 38 x 35 μm (34-39 x 27-37 μm); tectum continuous.

B. asiatica Roxb. ex DC. var. *asiatica* (Fig. 5-8)

Grains spiraperturate, spiral single, perfect, continuous, coils round the grain winding parallely to delineate the surface into a perfect continuous strip; aperture margin smooth. Exine 3 μm thick, ectoexine thicker than the endoexine; surface foveolate-fossulate, with LO-OL pattern, columella indistinct. Grains prolate-spheroidal, 32-47 x 27-36 μm; AMB-circular.

Note : There are two varieties in *B. asiatica* viz., var. *asiatica* and var. *clarkiana*, but in the taxonomic treatment of this taxa the authors could not differentiate between the two varieties morphologically due to paucity of specimens. Using pollen morphological studies of various specimens a distinct pollen morphotype was encountered in one of the specimens which differed from the others in some key characters mentioned below.

Key to varieties

1. Surface foveolate-fossulate with-LO pattern; grains prolate-spheroidal, 32 x 27 μm ..... a. *B. asiatica* var. *asiatica*
1. Surface punctate with - OL pattern; grains prolate, 47 x 36 μm ..... b. *B. asiatica* var. *clarkiana*

B. Chitria Lindl. (Fig. 9-12)

Grains spiraperturate, spiral curved, rarely bifurcates with ends coalescing, sometimes the spiral crosses in such a manner as to delimit the grain into 2-3 tightly interlocked pieces; aperture narrow, margin baculate with heterogenous baculae spreading along the margin. Exine 2.5 - 3 μm thick, ectoexine thicker than the endoexine; surface punctate to foveolate-fossulate with - OL pattern having dense heterogenous, circular, oblong or fossulate perforrations; columella faint; tectum perforrate. Grains spheroidal, sub-spheroidal or prolate-spheroidal; size varies, 40 μm diam or 38-48 x 37-38 μm in prolate spheroidal grains.

Key to varieties

1. Grains spheroidal/sub-spheroidal; diam 40 μm; surface punctate ..... a. *B. chitria* var. *chitria*

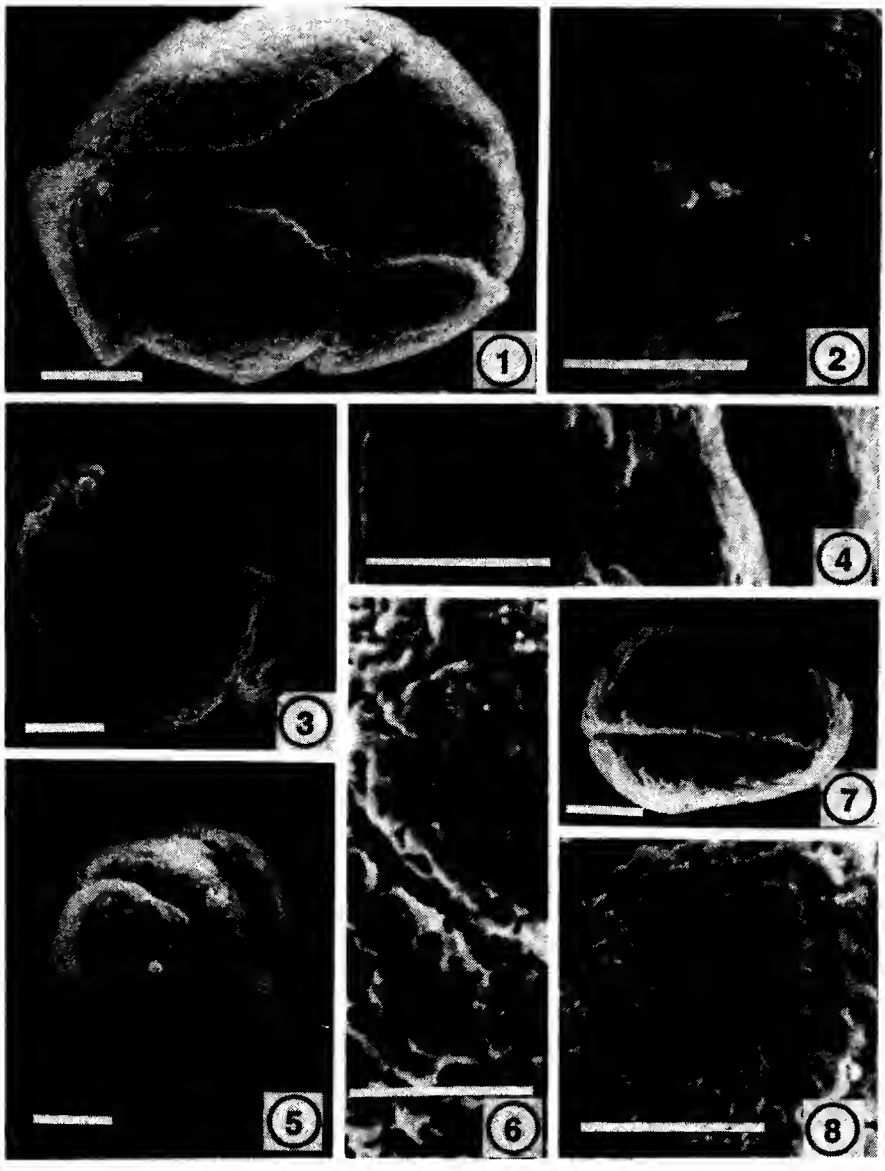

Fig. 1-8, Scanning electron micrographs of pollen of *Berberis*. 1-2 : *B. apiculata*, 1 : pollen with curved spiral, 2 : surface striato-punctate surface pattern. 3-4 : *B. aristata*, 3 : 3-colpate pollen with sunken colpi, 4 : psilate-smooth surface pattern. 5-8 : *B. asiatica*, 5-6 : var. *asiatica*, 5 : pollen showing a perfect spiral 6 : foveolate-fossulate surface, 7-8 : ± var. *clarkiana*, 7 : spiraperturate pollen 8 : punctate surface. (Scale lines = 10 μm in full grains, 5 μm in surface enlarged).

1. Grains prolate spheroidal; 45 x 37 μm; surface fossulate ..... b. *B. chitria* var. *occidentalis*

Note : Based on pollen morphological characters var. *occidentalis* has been seggregated from var. *chitria*. This is in contradiction to the morphological characters where these two varieties have been kept under one.

B. coriaria Royle ex Lindl. (Figs. 13-16)

Grains spiraperturate; spiral complex, curved and branched irregularly, delineating the surface into 4-5 elongated plates, sometimes spiral crosses the inter-apertural area horizontally/ longitudinally; aperture wide, membrane rough, margin smooth. Exine 1.5-3 μm thick; ectoxine equal to endoexine; surface psilate-rough or punctate with heterogenous interconnected punctae; Grains spheroidal; 35 μm diam (+ 2 μm) AMB - circular, columella indistinct; grains tectate, tectum continuous.

Key to varieties

1. Surface psilate-rough; exine 3 μm thick ..... a. *B. coriaria* var. *coriaria*
1. Surface puncate with heterogenous interconnected punctae; exine 1.5 μm thick ..... b. *B. coriaria* var. *patula*

B. dasyclada Ahrendt (Figs. 17-18)

Grains spiraperturate; spiral continuous, dividing the surface into cross-strips; aperture margin coarse; membrane granulate at places, granules heterogenous; ends rounded. Exine 2.2-3 μm thick, with ectoexine equal or thicker than endoexine; surface smooth distantly punctate with slightly elongated perforations. Grains subsperoidal, 56 x 52 μm (range 54-60 x 50-54 μm), AMB circular-oval, columella faint, tectum perforate.

B. griffithiana Schneid. (Fig. 19-22)

Grains spiraperturate, spiral irregularly twines dileneating the sufface into elongated and rounded areas; aperture narrow, margin smooth. Exine 3 μm thick, ectoexine thicker than the endoexine, columella, columella indistinct; surface coarse, organized into irregular raised lumps of piloid elements, or warted. Grains spheroidal, diam 40 μm (32-42 μm) AMB - circular, tectum irregular.

Key to varieties

1. Grains spheroidal; diam 34 μm; surface with closely packed, homogenous, piloid elements ..... a. *B. griffithiana* var. *griffithiana*
1. Grains sub-spheriodal; 37 x 40 μm; surface warted ..... b. *B. griffithiana* var. *pallida*

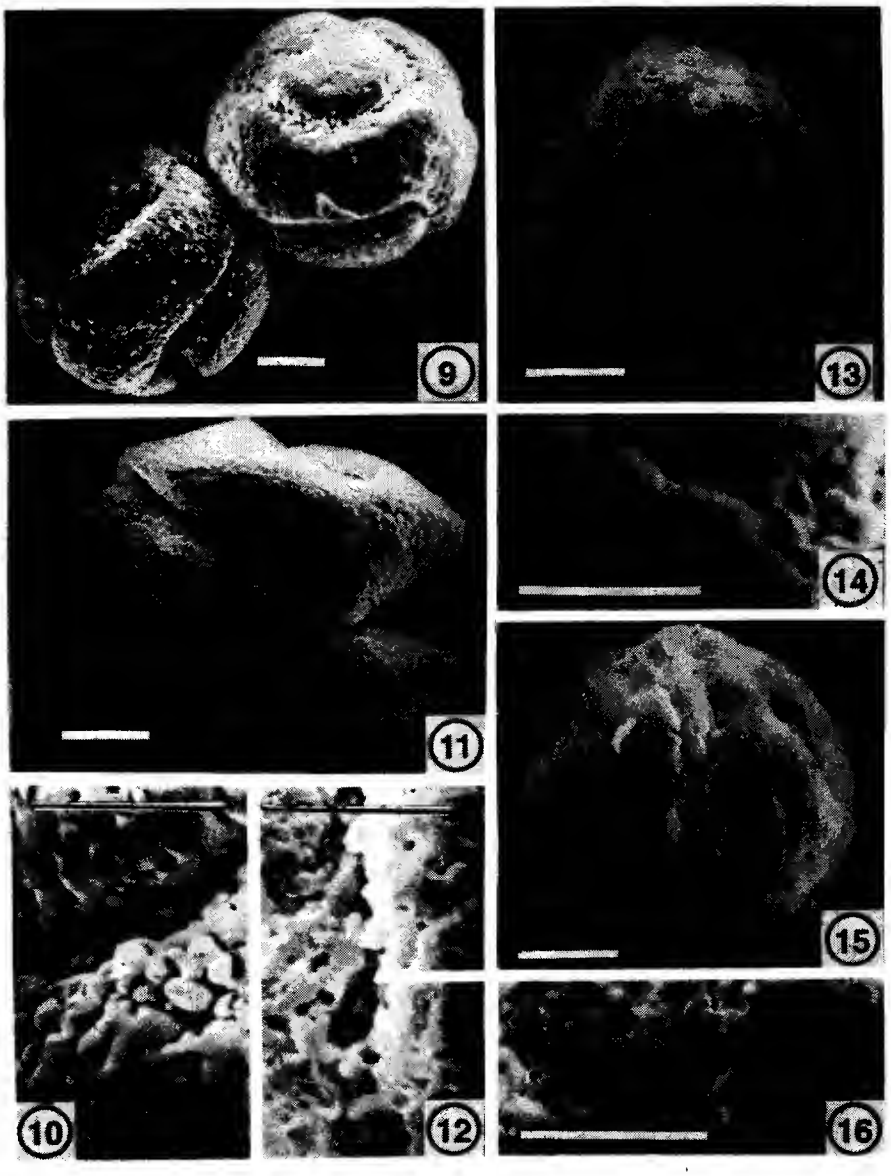

Fig. 9-16, Scanning electron micrographs of pollen of *Berberis*. 9-12 : *B. chitria*, 9-10 : var. *chitria*, 9 : grains showing var iously curved spiral, 10 : punctate surface, 11-12 : var. *occidentalis*, 11 : prolate pollen, 12 : fossulate surface. 13-16 : *B. coriaria*, 13-14 : var. *coriaria*, 13 : pollen with surface dileneated into 4-5 elongated plates, 14 : psilate-rough surface, 15-16 : var. *occidentalis*, 15 : pollen with longitudinally crossing spiral, 16 : surface with inter connected punctae. (Scale lines = 10 μm in full grains, 5 μm in surface enlarged).

B. hamiltoniana Ahrendt (Fig. 23-24)

Grains spiraperturate, spiral continuous, unbranched, elongated, winds back on itself in a 'U' fashion, completely encircling the grain; sometimes delineates a circular area on the surface; aperture margin thin, uneven. Presence of one or two pores (with endopore). Exine 2.5 μm thick, endoexine almost twice as thick as the ectoexine. Surface rough with small dense groups of islands separated by rounded, circular or elongated depressions, grains sub-speroidal, 23 x 21 μm (21-24 x 20-22 μm). AMB - circular, columella indistinct, tectum continuous.

B. incrassata Ahrendt (Fig. 25-26)

Grains spiraperturate; spiral elongate, winding variously often circular spirals occur, delineating the surface into elongated, irregular or circular areas, margin smooth and uneven, membrane smooth, ends acute. Exine 1.7 μm thick, endoexine thicker than ectoexine, columella indistinct; surface smooth with weak, rounded and homogenous perforations. Grains prolate - spheroidal to subprolate, 62.5 x 57.5 μm; AMB circular, tectum perforate.

B. insignis Hk. f. & Thoms. (Fig. 27-30)

Grains 3-4 colpate colpi broad, sycolporization of colpi sometimes forms a ring like "spiroid" aperture which divides the grain into 2 unequal, conjoint halves, alongwith 1-2 free colpi; colpus margin coarse, membrane rough, tip blunt; 2-3 μm wide. Exine 3 μm thick; ectoexine thicker than endoexine, columella faint; surface psilate or with sparsely dispersed small puntae (-OL pattern) Grains-spheroidal/sub-spheroidal, 39 x 42 μm (range 34-43 x 36-44 μm), tectum perforate.

Key to varieties

1. Surface psilate; grains spheroidal, diam 40 μm ..... a. *B. insignis* var. *insignis*
1. Surface punctate; grains sub-spheroidal, 39 x 42 μm ..... b. *B. insignis* var. *shergaonensis*

B. jaeschkeana Schneid. (Figs. 31-37)

Grains spiraperturate, spiral long continuous, sometimes cutting off small branches, delineates the surface tint elongated longitudinal or transverse strips; usually broad, margin smooth, tips acute. Exine 1.5-3 μm thick, ectoexine equal to or slightly thicker than the endoexine; surface foveolate-punctate with dense punctae or psilate, columella faint. Grains spheroidal with 35 μm diam or subprolate, 53 x 46 μm (50-54 x 44-47 μm) AMB-oval, tectum discontinuous.

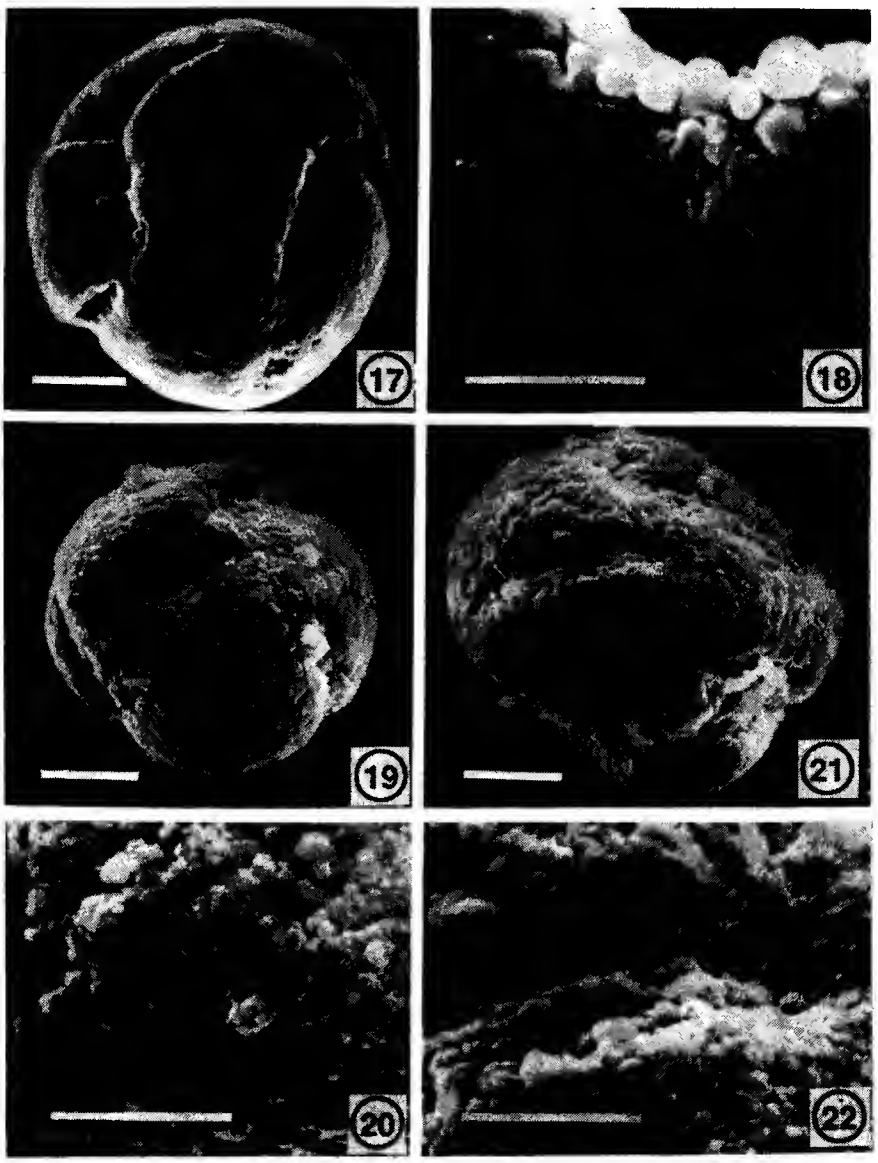

Fig. 17-22, Scanning electron micrographs of pollen of *Berberis*. 17-18 : *B. dasyclada*; 17 : pollen with traversely crossing spiral, 18 : sparsely punctate surface 19-22 : *B. griffithiana*, 19-20 : var. *griffithiana*, 19 : surface view, 20 : surface with homogenous piloid groups, 21-22 : var. pallida 21 : surface view, 22 : warted surface. (Scale lines = 10 μm in full grains, 5 μm in surface enlarged).

Key to varieties

1. Surface foveolate-punctate, grains sub-prolate, 53 x 46 μm
2. Spiral 'U' shaped ..... a. *B. jaechkeana* var. *jaeschkeana*
2. Spiral 'S' shaped ..... b. *B. jaechkeana* var. *usteriana*
1. Surface psilate, grains spheroidal, diam 35 um ..... c. *B. jaechkeana* var. *bimblica*

B. kashmiriana Ahrendt (Figs. 38-39)

Grains spiraperturate, spiral undulating, sharpely turns on inself two to three times in 'U' shape, encircling the entire grain to divide the surface into collateral halves, aperture narrow, margin slightly wavy. Exine 2.5 μm thick, endoexine thicker than ectoexine, columella invisible; surface roughly warted with densely packed, irregular islands. Grains prolate, 44 x 37 μm (42-45 x 35-38 μm) AMB oval, tectum continuous.

B. koeheneana Schneid. (Figs. 40-42)

Grains irregularly polycolpate; colpi zonal or irregular, of varying length, membrane baculate, bacula heterogenous, margin rough, ends ill-defined; poral complex also occurs alongwith the colpi; pore annulate, diam 10 μm, membrane baculate, endopore 3-4 μm, margin rough. Exine 2.5-3 μm thick, endoexine thicker than endoexine; surface foveolate with fossulate perforrations, columella faint. Pollen diam 40 μm (38-43 μm); spheroidal; tectum present; AMB circular.

B. kunawurensis Royle var. *kunawurensis* (Figs. 43-44)

Grains inaperturate; 3-4 broadly colpoid zones on the surface mark the apertural region. Exine 2 μm thick; ectoexine almost as thick as the endoexine; columella faint; surface roughly foveolate. Grains spheroidal; 30 μm diam (29-32 μm); tectate.

B. lycium Royle (Figs. 45-52)

Aperture 3-4 colpate or spiraperturate; colpi may be free or united at the polar ends tending towards syncolporization; in spiraperturate grains the spiral may be simple or forming a loop delimiting the surface into a single strip or cross strips; apertural width 1.5-6 μm, membrane smooth, margin thin or may be thickened to form a raised margo. Exine 1.7-3 μm thick; ectoexine equal to or slightly thicker than the endoexine, columella indistinct; surface foveolate, punctate or fossulate or with an undefined rough pattern. Grains spheroidal, subprolate or prolate in shape; 30-40 μm in diam or 30 x 25 (± 3 μm) to 40 x 32 μm (± 3 μm). AMB - Circular or oval; tectum present, perforrate in punctate grains.

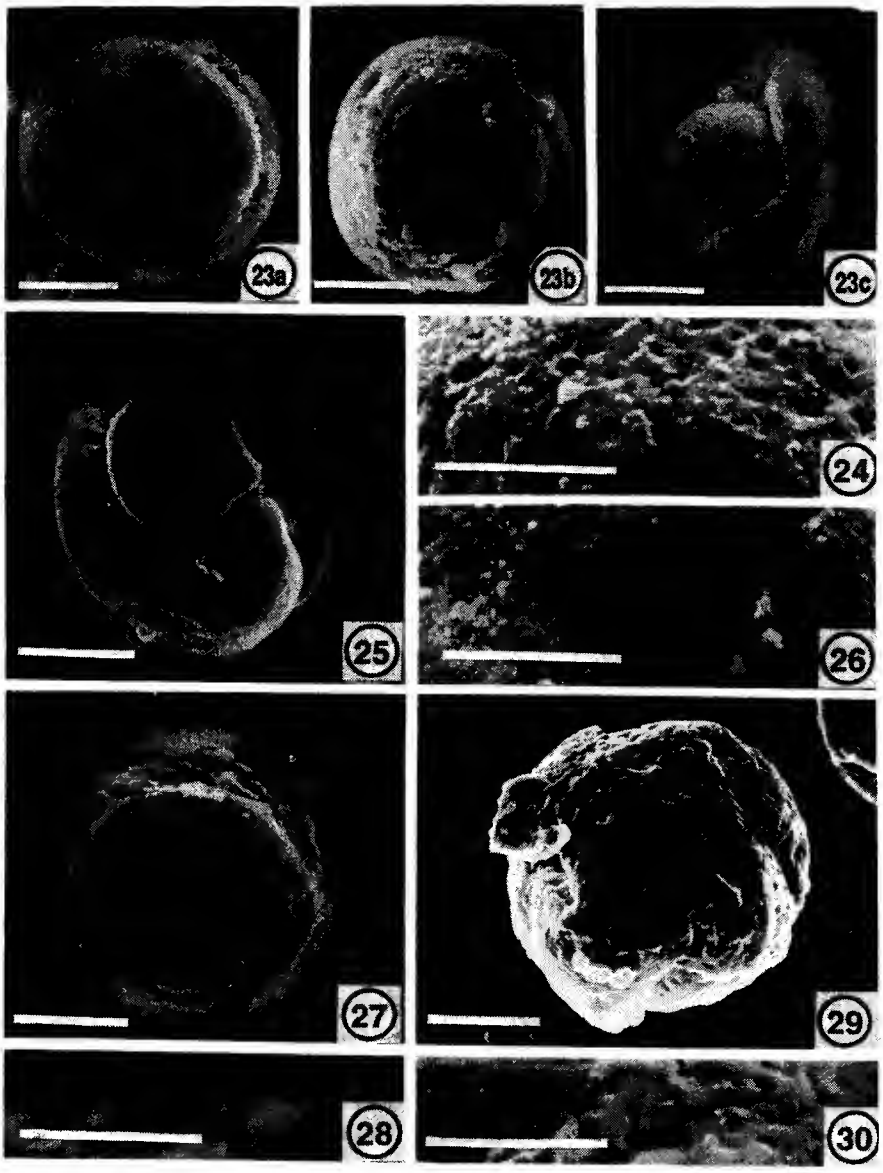

Fig. 23-30, Scanning electron micrographs of pollen of *Berberis*. 23-24 : *B. hamiltoniana*, 23 : circular spiral, 24 : rough surface, 25-26 : *B. incrassata*, 25 : pollen with a circular spiral, 26 : weakly perforrate surface, 27-30 : *B. insignis*, 27-28 : var. *insignis*, 27 : pollen with spiroid aperture, 28 : psilate surface, 29-30 : var. *shergaoenensis*, 29 : pollen with spiroid and free colpi, 30 : punctate surface (Scale lines = 10 μm in full grains, 5 μm in surface enlarged).

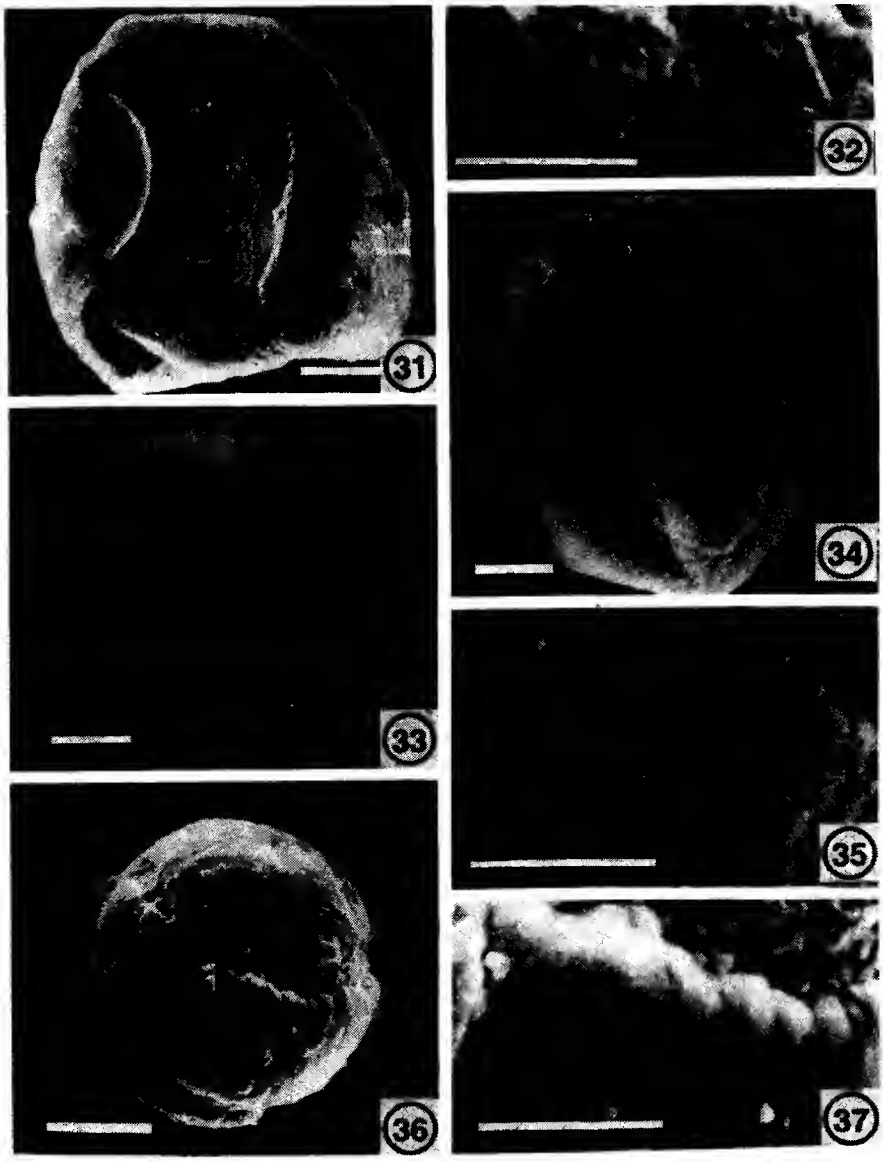

Fig. 31-37, Scanning electron micrographs of pollen of *Berberis*. *B. jaeschkeana*, 31-32 : var. *jaeschkeana*, 31 : pollen with 'U' shaped spiral, 32 : foveolate-punctate surface, 33-35 : var. *usteriana* 33-34 pollen with 'S' shaped spiral, 35 : foveolate-punctate surface, 36-37 : var. *bimblica*, 36 : spheroidal pollen, 37 : psilate surface pattern (Scale lines = 10 μm in full grains, 5 μm in surface enlarged).

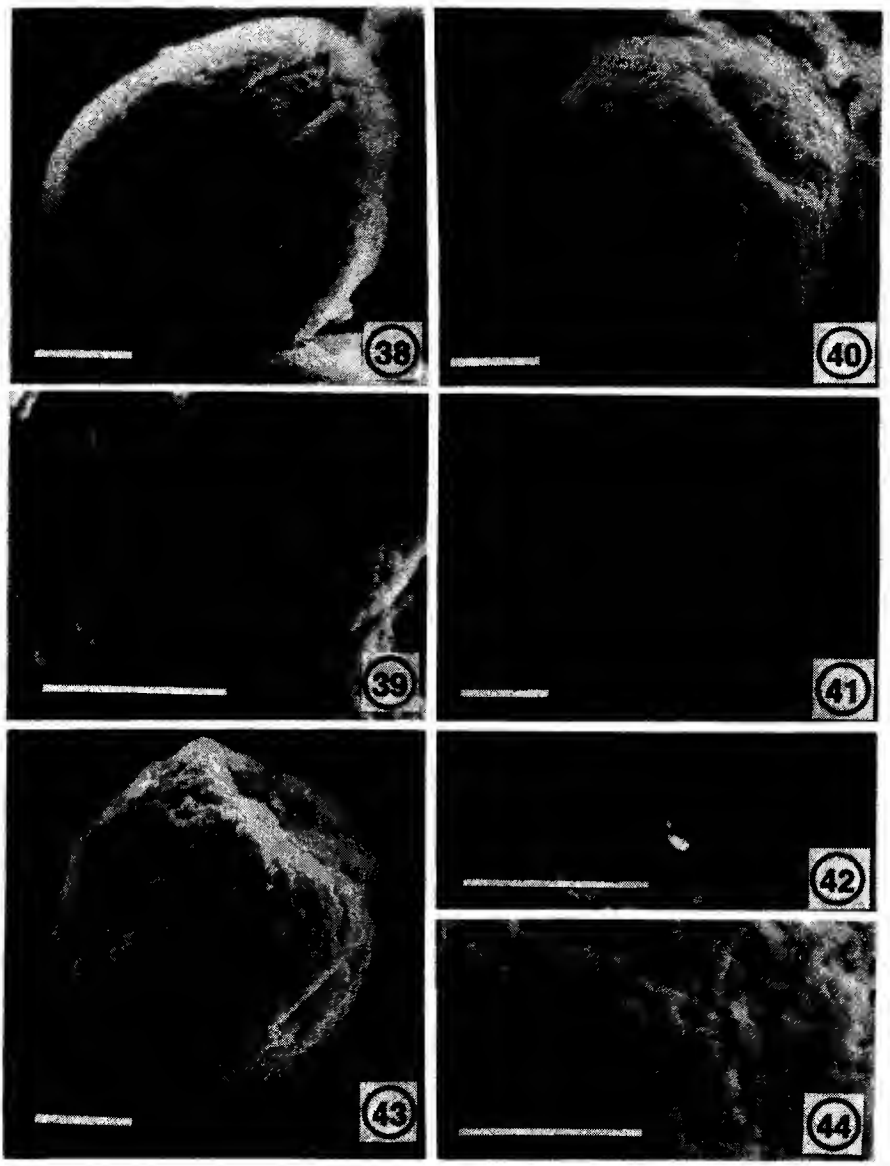

Fig. 38-44, Scanning electron micrographs of pollen of *Berberis*. 38-39 *B. Kashmiriana*, 38 : pollen showing spiral undulating in 'U' shape, 39 : roughly warted surface, 40-42 : *B. koeheneana*, 40 : pollen with 2 colpi and one pore, 41 : pollen with 2 colpi showing piloid apertural membrance, 42 : fossulate surface. 43-44 : *B. kunawurensis*, 43 : pollen with colpate zones, 44 : roughly foveolate surface (Scale lines = 10 μm in full grains, 5 μm in surface enlarged).

Palynology of *Berberis*

Key to varieties

1. Grains sub-prolate; aperture 1.5-2 μm wide.
2. Surface faintly foveolate-fossulate; average pollen size 40 x 33 μm ..... a. *B. lycium* var. *lycium*
2. Surface foveolate-punctate; avg. pollen size 30 x 25 μm ..... b. *B. lycium* var. *simlensis*

1. Grains spheroidal; aperture 4-6 μm wide.

3. Surface faintly perforrate; pollen diam 30 μm ..... c. *B. lycium* var. *subfascicularis*
3. Surface with undefined pattern; pollen diam 40 μm ..... d. *B. lycium* var. *subvirescens*

B. macrosepala Hk.f. & Thoms. (Figs. 53-56)

Grains inaperturate; or with ill-defined openings on the surface which denote the germinal sites. Exine 1.5 μm thick; ectoexine thicker than the endoexine; columella indistinct, surface rough with irregular exine folds or roughly punctate. Tectum indistinct; grains spheroidal; diam 27-33 μm (25-33 μm); AMB-circular.

Key to varieties

1. Surface roughly punctate; pollen diam 27 μm ..... a. *B. macrosepala* var. *macrosepala*
1. Surface rough with irregular folds and few punctate; pollen diam 33 μm ..... b. *B. macrosepala* var. *sakdenensis*

B. pachyacantha Koehne var. *pachyacantha* (Figs. 57-58)

Grains spiraperturate, spiral undulating, often 'S'-shaped, sometimes interrupted by exine channels; aperture 3-4 μm wide, tips acute, membrane smooth, margin gemmate, gemmae heterogenous, sometimes spreading across the aperture. Exine 2-3 μm thick; endoexine thicker than ectoexine, columella faint; surface reticulo-punctate, punctae heterogenous, rounded or elongated. Grains spheroidal, diam 35 μm (32-36) AMB-circular, tectum perforate.

B. petiolaris Wall. ex G. Don (Figs. 59-62)

Grains panto-polycolpate; colpi very long and curved encircling a part of the grain, sometimes syncolporization may occur to form a 'spiroid' ring; margin smooth - wavy, width 1 μm, Exine 2-2.2 μm thick; ectoexine equal to or thicker than the endoexine; surface psilate-smooth or sparsely punctate with fine holes. Grains spheroidal or irregular, 32 μm diam (30-35 μm); tectate.

Key to varieties

1. Grains spheroidal; surface psilate smooth ..... a. *B. petiolaris* var. *garhwalana*
1. Grains irregular, surface sparesely punctate ..... b. *B. petiolaris* var. *extensa*

B. praecipua Schneid. (Figs. 63-65)

Grains panto-polycolpate; colpi short, sunken, interrupted by exine foldings, 1.5-2 x 10-12 μm, ends acute or extending, margo thickend. Exine 2.5 μm thick, ectoexine thicker than endoexine; columella faint; surface rough, sparsely punctate, homogenous. Grains sub-sheroidal; 32 x 30 μm (32-34 x 30-33 μm); AMB-oval.

B. replicata W.W. Smith var. dispar (Figs. 66-67)

Grains inaperturate, one or two colpoid streaks occur in association with irregular fissures of exine surface. Exine 1.7 μm thick; ectoexine equal to endoexine, columella indistinct; surface psilate, smooth with irregular folds. Grains spheroidal; diam 45 μm (44-47 μm); tectum illdefined; AMB-circular.

B. sanei Husain et. al. (Figs. 68-71)

Grains 3-4 colpate, colpi long, crossing the entire grain, sometimes syncolporization of adjacent or opposite colpi unite to form a "spiroid" aperture or a 'semi-spiral' which delimits the surface into 'U'-shaped curved strips colpi margin smooth, membrane smooth, tips blunt or ill defined. Exine 2.2 μm thick, endoexine twice thicker than ectoexine, columella indistinct, surface faintly and densely reticulo-punctate (with a negative reticulum) with very minute fine holes having - OL pattern, psilate at places, linear-thread like sporopollenin thickening also present. Grains prolate spheroidal, 67 x 62 μm (65-69 x 56-55 μm) AMB-ciruclar-angulate; tectum perforate.

PHYLOGENETIC CONSIDERATIONS OF *BERBERIS*

Pollen morphology can be grouped into five categories namely, apertures, exine ornamentation, exine strata, size and shape in order of their phylogenetic significance. Of these, the germinal apertures bear genetically stable characters and to a great extent convey the phylogenetic status of the taxon/species. Owing to this consistency in pollen-spore morphology, the apertural characteristics are considered primary, exine ornamentation secondary, and other characters tertiary in terms of phylogenetic values (Nair, 1970, 1987-88).

1. Apertural Evolution

According to Walker and Doyle, (1975) evidence from extant primitive angiosperms suggest that inaperturate, not trichotomosulcate (Stracker, 1963; Wilson, 1964) was the ancestral

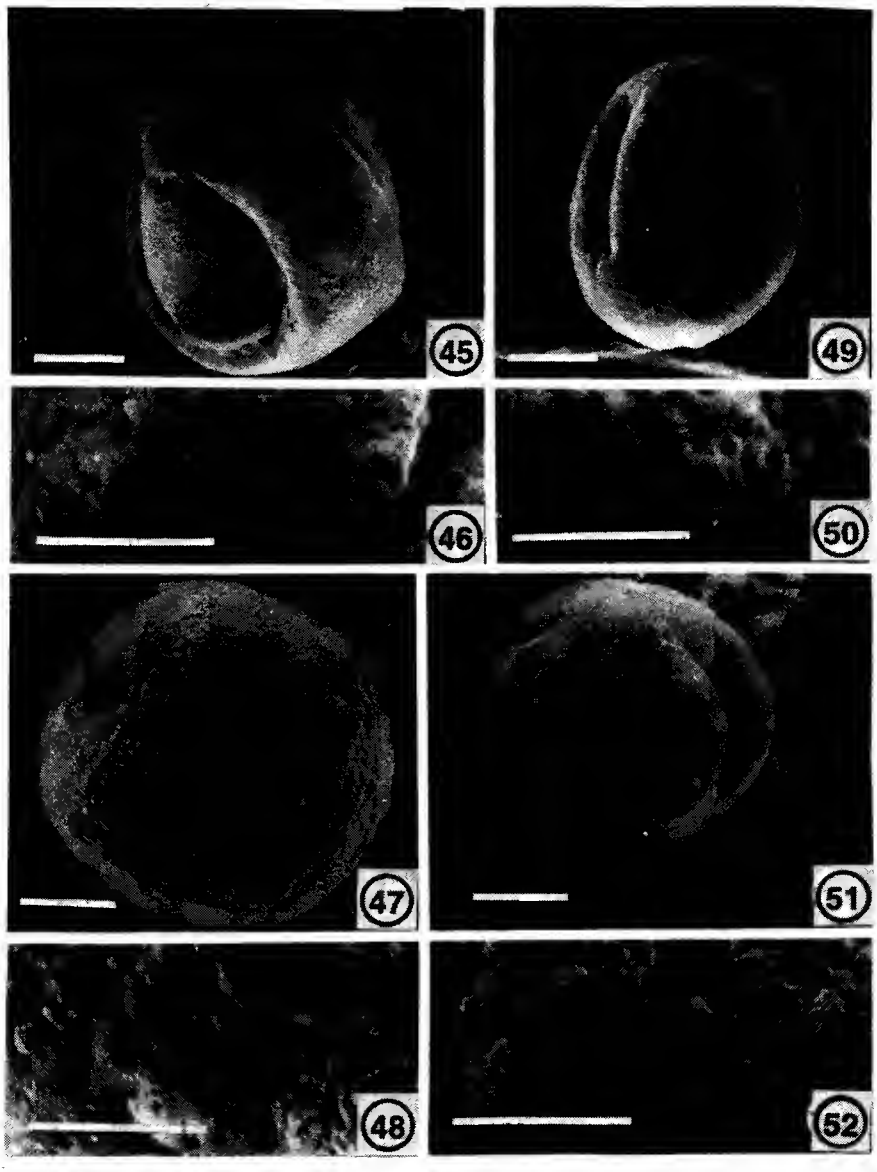

Fig. 45-52, Scanning electron micrographs of pollen of *Berberis*. *B. lycium*, 45-46 : var. *lycium*, 45 : pollen with loopforming aperture, 46 : mildly foveolate-fossulate surface, 47-48 : var. *subfascicularis*, 47 : spiraperturate pollen, 48 : faintly perforrate surface, 49-50 : var. *simlensis*, 49 : 3-4 colpate pollen, 50 : foveolate-punctate surface, 51-52 : var. *subvirescens*, 51 : 3-4 colpate pollen, 52 : rough undefined surface (Scale lines = 10 μm in full grains, 5 μm in surface enlarged).

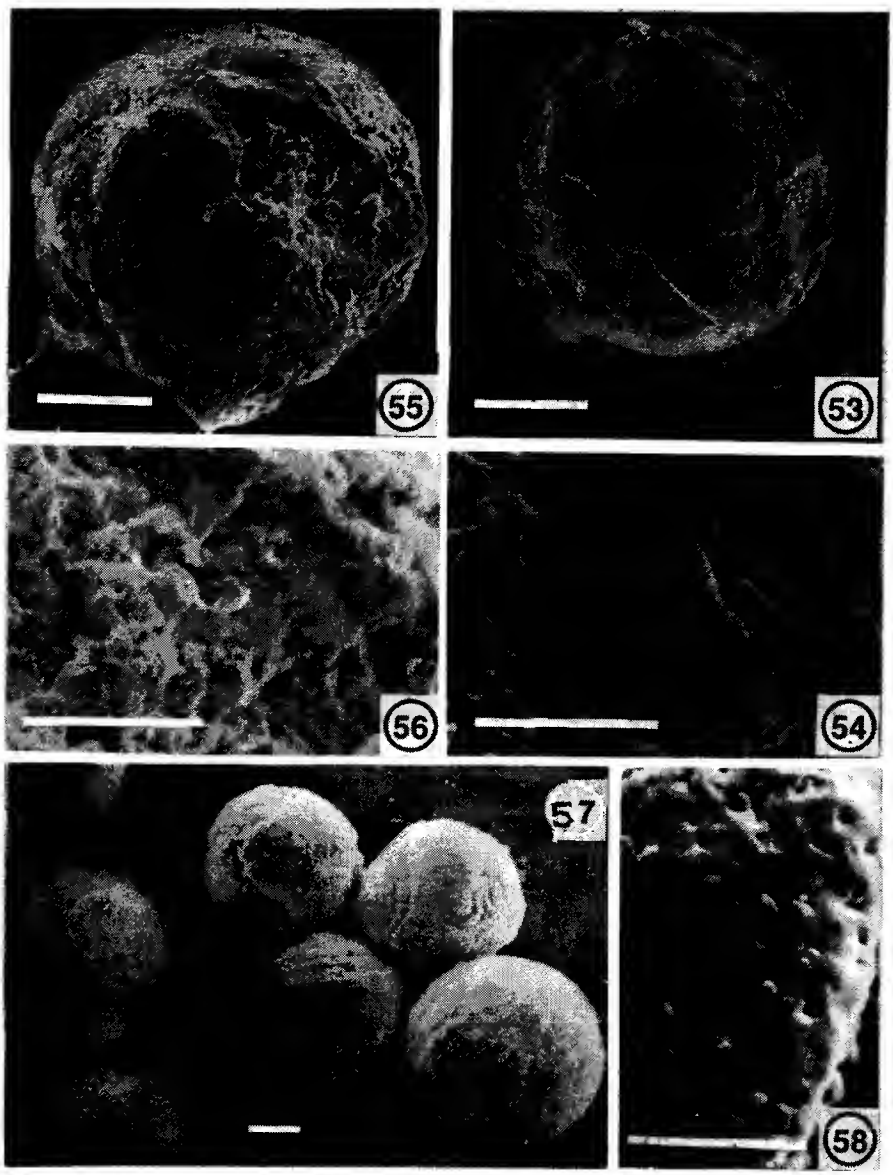

Fig. 53-58, Scanning electron micrographs of pollen of *Berberis*. 53-56 : *B. macrosepala*, 53-54 : var. *macrosepala*, 53 : inaperturate pollen, 54 : roughly punctate surface, 55-56 : var. *sakdenensis*, 55 : inaperturate pollen, 56 : rough surface with irregular germinal sites (Scale lines = 10 μm in full grains, 5 μm in surface enlarged).

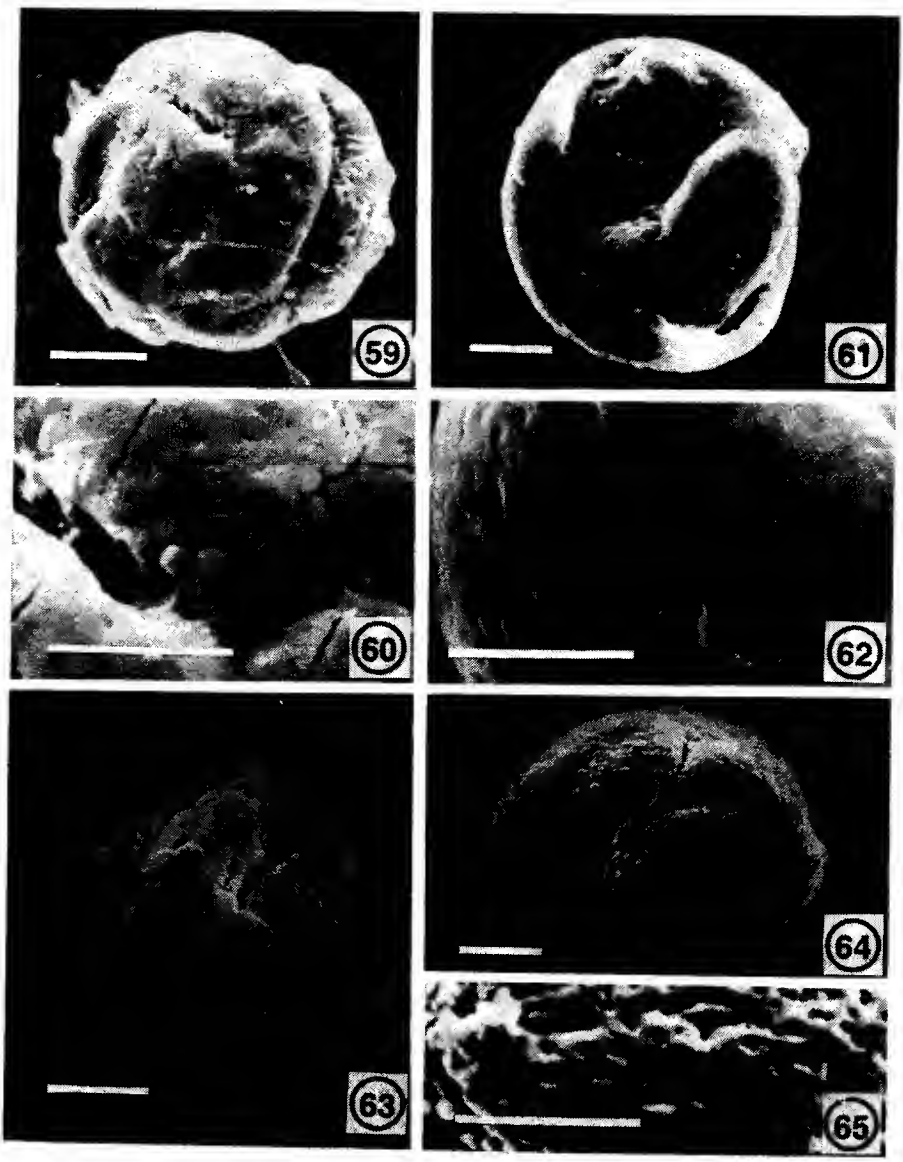

Fig. 59-65, Scanning electron micrographs of pollen of *Berberis*. 59-62; *B. petiolaris*, 59-60 : var. *garhwalana*, 59 : pantocolpate pollen, 60 : psilate-smooth surface, 61-62 : var. *extensa*, 61 : pollen with a spiroid ring, 62 : sparsely punctate surface, 63-65 : *B. praecipua*, 63 : pollen with short sunken colpi, 64 : pollen with one colpus extending to poles, 65 : sparsely punctate surface. (Scale lines = 10 μm in full grains, 5 μm in surface enlarged).

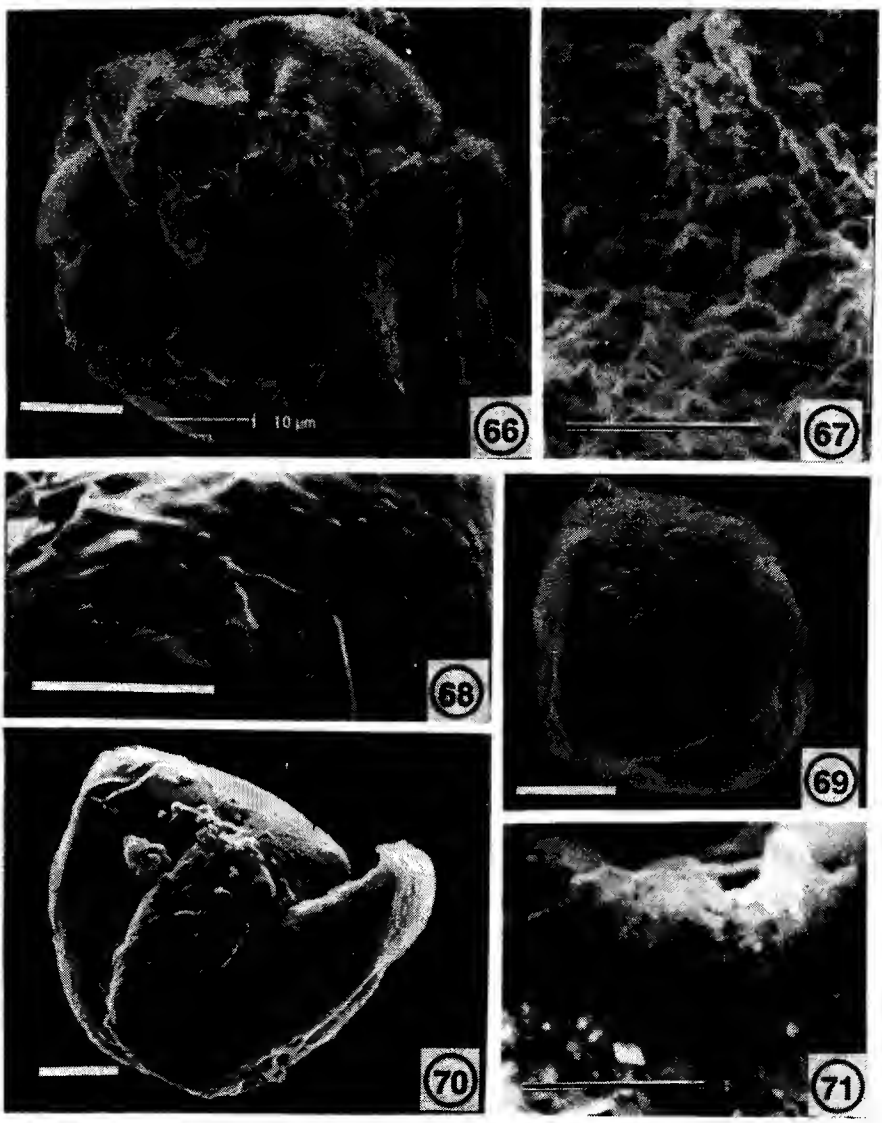

Fig. 66-71, Scanning electron micrographs of pollen of *Berberis*. 66-67 : *B. replicata* var. *dispar*, 66 : pollen showing cracks and fissures on surface, 67 : ill-defined psilate surface, 68-71 : *B. sanei*, 68 : pollen with spiroid aperture, 69 : 3-colpate pollen, 70 : psilate area of the surface, 71 : punctate area with thread like thickening. (Scale lines = 10 µm in full grains, 5 µm in surface enlarged).

pollen type which gave rise to the uniquely angiospermous (dicotyledonous) colpate pollen aperture, and from the basic tricolpate form of this colpate pollen diverse types - 5-6 colpate, porate, colporate apertures evolved. Phylogenetically, he classified pollen with respect to the number of apertures as, (I) inaperturate (2) mono-aperturate (3) disaperturate (4) tri-aperturate or (5) polyaperturate with 4,5,6 apertures, and aperture shape as elongate, furrow like round, pore like or encircling ring or band like.

In *Berberis* pollen the apertural system shows a complete series from inaperturate to perfectly spiraperturate condition (Tables 2, 3). The extremes of this series are represented by *B. macrosepala* (inaperturate) and *B. asiatica* (perfectly spiraperturate). All the other forms demonstrate different degrees of evolutionary levels with advancement towards syncolporization. Some grains may be considered irregularly syncolpate rather than spiraperturate but the two conditions intergrade, as in *B. lycium*. *Berberis lycium* represents a connecting link between the syncolpate and spiraperturate forms having a highly variable apertural condition. The species possesses 3-4 colpate, syncolpate or spiraperturate pollen with broken or complete spiral (Figs. 45-52).

The species of *Berberis* which fall intermediate to the two extremes possess varying proportions of 3 colpate to polycolpate (*B. aristata, B. koeheneana, B. praecipua,* syncolpate (*B. insignis, B. petiolaris*), spiroid (*B. sanei*) apertures followed by branched spirals with free or coalescing ends to cut off circular or irregular areas of the surface as in *B. chitria, B. coriaria* and *B. apiculata*. The unbranched spiraperturate forms are represented by *B. hamiltoniana, B. jaeschkeana, B. pachyacantha, B. dasyclada, B. incrassata, B. griffithiana* and *B. kashmiriana* with varying degrees of advancement culminating in the perfectly spiraperturate grains of *B. asiatica* (Tables 2, 3). The range of apertural types when observed in descending series are, perfectly helicoid spiral (*B. asiatica*), spiral dividing the grain into two collateral halves (*B. kashmiriana*) and 3-zone/panto-colpate apertures (*B. sanei*) and inaperturate condition (*B. macrosepala*), and vice versa.

Spiral or colpus found in combination with a pore complex as in *B. hamiltoniana* and *B. koeheneana* respectively represent a specialised condition in *Berberis* which has probably arisen due to some ontogenetic accident during syncolporization, perhaps by excessive curving of the colpus.

From the ongoing discussion it may be concluded that origin of spiraperturate condition in *Berberis* is monophyletic. The basic pollen types are inaperturate pollen with cracks and breaks or fissures on the surface denoting apertural zones. From this type emerged the 3-4 colpate and polycolpate forms leading to syncolpate condition by progressive colporization of the apocolpia. Further winding and syncolporization lead to the spiroid apertures which modified to form perfect spirals as in *B. asiatica*.

According to Furness (1985) the spiraperture is a derived aperture type which has arisen independently from different ancestors in various plant groups, probably as a result of an ontogenetic

Table 2 : Pollen Morphotypes in *Berberis*

Taxa	Aperture	Pore -/+	Surface Ornamentation	Exine in µm	P(L)	E(S)	P/E	Pollen Shape	-OL/-LO
B. apiculata	curved vairously	-	striato-punctate	2	52	40	1.3	sub-prolate	- OL
B. aristata	3-colpate	-	psilate-smooth	6/9	38(L)	35(S)	1.52	irregular	- LO
B. asiatica	perfect, single	-	foveolate-fossulate	3	32/47	27/36	1.19	prolate-spheroidal	- LO
B. chirtia	curved	-	punctate, foveolate fossulate	2.5-3	40/45	37	1.02	spheroidal/sub-spheroidal/prolate	- OL
B. coriaria	branched	-	psilate rough	2.5-3	35	35	1	spheroidal	- LO
B. dasyclada	transverse crossing	-	sparsely punctate	2.2-3	56	52	1.07	sub-spheroidal	- LO
B. griffithiana	irregularly twining	-	coarse, in groups or warted	3	34/40	34/40	1	sub-spheroidal/ spheroidal	- LO
B. hamiltoniana	continuous 'U' shape	-	rough, in groups	2.5	22	21	1.04	sub-spheroidal	- LO
B. incrassata	variously curving	-	psilate-weakly punctate	1.7	62	57	1.09	prolate-spheroidal	- OL
B. insignis	3-4 (syn-1) colpate	-	psilate/punctate	3	39	42	0.93	spheroidal/ sub-spheroidal	- OL
B. jaechkeana	variably winding	-	foveolate-punctate/	1.5-3	35/53	35/46	1-1.15	spheroidal/ sub-spheroidal	- OL
B. kashmiriana	undulating or 'U' shaped	-	roughly warted	2.5	44	37	1.19	prolate	- LO
B. koeheneana	polycolpate	+	foveolate-fossulate	2.5-3	40	40	1	spheroidal	- LO
B. kunawurensis	inaperturate, 3-4 colpoid zones	-	roughly foveolate	2	30	30	1	spheroidal	- LO
B. lycium	rings or loop/ often interrupted	-	foveolate	1.7-3	30-40	25-35	-	spheroidal to prolate	- LO
B. macrosepala	inaperturate	-	rough or roughly punctate	1.5	33	33	1	spheroidal	- LO
B. pachyacantha	spiral 'S' shaped	-	reticulo-punctate	2-3	35	35	1	spheroidal	- OL
B. petiolaris	panto-poly-colpate		psilate smooth to sparsely punctate	2-2.2	32	32	1	spheroidal	-LO/-OL
B. praecipua	panto-poly-colpate	-	roughly, sparsely punctate	2.5	32	30	1.06	sub-spheroidal	- OL
B. replicata	inaperturate, 1-2 colpoid streaks	-	psilate, ill-defined	1.7	45	45	1	spheroidal	--
B. sanei	3-4 colpate	-	reticolo-punctate/ psilate	2.2	67	62	1.08	prolate spheroidal	- OL

Table 3 : Apertural Evolution in *Berberis* Pollen

	Type	Taxa	Apertural Configuration	Surface Dileneation	Memberane	Margin	Width in µm	Evol. level
Inaperturate	Crack, Fissures & colpoid streaks	*B. macrosepala*	undefined	---	---	---	-	Primitive
		B. replicata	1-2 colpoid streaks, irregular fissures	---	---	---	-	
		B. kunawurensis	3-4 colpoid streaks	---	---	---	-	
3-4 Pantocolpate	3-4 CO LP AT E	*B. aristata*	3-4 zonal or irregular colpi, sunken	---	---	thick folded on colpus	6-9	B A S I C
		B. insignis	syncolporate with 1-2 free colpi	2 unequal, conjoint halves	rough	coarse	-	
		B. sanei	spiroid, and free colpi	curved 'U' shaped areas	baculate	smooth	2-3	
	PO LY CO LP AT E	*B. petiolaris*	panto-/poly-colpate	---	smooth	smooth wavy	1	
		B. praecipua	panto-/poly-colpate sunken colpi	---	---	thick	3	
		B. koeheneana	polycolpate with irregular colpi	---	baculate, heterogenous	rough	-	
	INTERM EDIATE	*B. lycium*	spiral simple/branched/ loop like/interrupted	circular of irregular strips or plate-like areas	smooth/ granular	variable smooth/ rough	2-4	

	Type	Taxa	Apertural Configuration	Surface Dileneation	Memberane	Margin	Width in µm	Evol. level
SPIRAPERTURATE	Brancded Spiral	*B. chitria*	curved & bifurcated ends coalescing	2-3 interlocked pieces	---	baculate	-	Intermediate
		B. apiculata	curved, rarely branched	4-6 irregular / elongated areas	---	smooth	-	
		B. coriaria	curved, irregularly branched	4-6 elongated plates	rough	smooth	-	
	Continuous Spiral	*B. hamiltoniana*	unbranched spiral, 'U' shaped; pore present	irregular bands	---	uneven, thin	-	ADVANCED
		B. pachyacantha	undulating 'S' shaped spiral	irregular bands	smooth	gemmate	3-4	
		B. kashmiriana	undulating 'U' shaped spiral	2 collateral parts	---	wavy	-	
		B. griffithiana	irregularly winding	elongated/rounded plates	---	smooth	-	
		B. incrassta	continuously winding	elongate/irregular/ circular areas	---	smooth	-	
		B. dasyclada	variably winding/ transverse (plagiotropic)	cross strips	granular	coarse	-	
		B. jaeschkeana	elongated, encircling the grain	longitudunal/ transverse strips	---	smooth	-	
	PERFECT SPIRAL	*B. asiatica*	perfect, parallel helicoid spiral	single long band	---	smooth	-	

accident and has been retained due to its adaptation to extreme environments which enable germination at numerous sites and thereby increases pollen germination rates and is therefore considered an advanced character. Contrary to his findings the present analysis on the apertural evolution in *Berberis* suggests that the spiraperture has arisen monophyletically and progressively from inaperturate and 3-colpate forms and has been retained for its advantageous adaptation in pollen germination.

2. Surface Ornamentation

With reference to exine sculpturing types primitive angiosperm pollen appeared to have been more or less psilate (Walker, 1975). Walker and Doyle (1975) classified the major exine sculpturin type as (1) psilate (2) foveolate (3) fossulate (4) scabrate (5) verrucate (6) baculate (7) psilate/clavate (8) gemmate (9) echinate (10) rugulate (11) striate and (12) reticulate.

The exine ornamentation in *Berberis* species ranges from foveolate to foveolate-fossulate. There are no projections. The punctae are of varying shapes and sizes ranging from very minute circular holes to rounded, oval, slightly elongated or irregularly shaped perforrations with smooth, rough, foveolate or wavy exine. The punctae may be heterogenous or homogenous and dense or sparse in an unorganised or reticulo-punctate fashion.

The evolutionary stages are as follows : roughly foveolate (*B. kunuwurensis*) → rough/psilate-smooth with sparse punctae (*B. praecipua* → smoothly/roughly punctate (*B. insignis*) → reticulo-punctae (*B. sanei*) → punctate with variable punctae (*B. apiculata*) → foveolate-fossulate (*B. asiatica*).

The evolution of surface ornamentation in *Berberis* appeared to be correlated with the apertural system of the pollen grain and is more or less parallel (with minute deviations) along the lines of the apertural evolution. The relation between apertural system and exine ornamentation is marked by inaperturate pollen with psilate-smooth surface of *B. macrosepala* on one end and the perfectly spiraperturate grains with foveolate-fossulate exine of *B. asiatica* on the other.

The "turning point" between smooth-punctate surface and foveolate-fossulate surface is marked by the striato/reticulo-punctate condition in *B. apiculata* and *B. sanei*.

3. Exine Strata

A thick undifferentiated exine is considered primitive to a thinner one (Nair, 1970). *Berberis* pollen has a thick exine (1.5-3μm, (upto 6 μm at apertural margins) with an amorphous undifferentiated tectum, columella and foot layer. Such an unstratified exine in the primitive genus represents an original unchanged state. Further, the thickened apertural margin as in *B. aristata* and *B. praecepoa* is considered primitive (Nair, 1987-88) to a thinner one and is an adaptation towards support of the germinal apertures.

4. Size and Shape

A larger grain is considered primitive to a smaller grain (Nair, 1970). In *Berberis* the pollen size is not related to apertural evolution. The smallest grains are found in *B. hamiltoniana* (23 x 21 μm) while the largest grains occur in *B. sanei* (67 x 62 μm). Most pollen are generally 35-45 μm in size.

Pollen shape corresponding to P/E ratio varies from spheroidal, sub-spheroidal, prolate-spheroidal to prolate. The spheroidal and sub-spheroidal forms are predominant (62%).

POLLEN MORPHOLOGICAL SUBDIVISIONS OF *BERBERIS*

On the basis of pollen morphology the genus *Berberis* can be subdivided into 3 groups :

Group I. Species with inaperturate pollen and psilate-smooth exine surface. The germinal sites are in form of crack breaks or fissures on the surface. Slight deviation of exine surface pattern is seen in *B. edgeworthiana* (roughly foveolate) but the grains are basically inaperturate.

Species included : *B. replicata, B. macrosepala* and *B. edgeworthiana*

Group II. Species with 3-polycolpate apertures exhibiting varying degree of syncolporization. The exine surface has sparse to dense punctae with minute intraspecific variations.

Species included : *B. petiolaris, B. praecipua, B. koeheneana, B. aristata, B. insignis*, and *B. sanei.*

Group III. Species with spiraperturate pollen. The exine ornamentation ranges from striato/reticulo-punctate with psilate or rough surface to foveolate-fossulate pattern. Variations of surface pattern are encountered in *B. coriaria* (psilate-rough), *B. hamiltoniana* and in *B. kashmiriana.* In view of the variability of the apertural system this group can be further subdivided into species with branched or unbranched spiral.

Species with branched spiral : *B. chitria, B. coriaria, B. apiculata, B. lycium.*

Species with unbranched spiral : *B. hamiltoniana, B. pachyacantha, B. kashmiriana, B. griffithiana, B. incrassata, B. dasyclada, B. jaeschkeana, B. asiatica.*

The species *B. lycium* falls in both Group II and in Group III as it possess variable pollen ranging from the basic 3-polycolpate to the advanced spiraperturate pollen in different varieties. Hence based also on apertural system this species may rightly be considered as a connecting link in the evolutionary history of the spiral aperture.

PALYNOLOGICAL RELATIONSHIP IN FAMILY BERBERIDACEAE WITH REFERENCE TO *BERBERIS*

The most comprehensive study of the pollen of Berberidaceae was first made by Kumazava (1936). He also included Ranunculaceae and Lardizabalaceae and provided descriptions and discussion for 46 genera and 230 species with 72 line drawing illustrations. He regarded *Berberis* and *Mahonia* pollen as inaperturate. Later in 1938 he established a Berberidaceae consisting of two subfamilies Berberidoideae with only *Berberis* and *Mahonia* and Epimedioideae with other genera, mainly on the basis of pollen morphology. Roland-Heydacker (1974) described the pollen of *Berberis vulgaris* L. and *Mahonia aquifolium* Nuttall as having unique helicoid colpi, as well as a compacted ektexine, a granular endexine and a persistant intine that reacted positively to tests for polysaccharides.

Nowicke and Skvarla (1981) reported that the two genera *Berberis* and *Mahonia* could not be distinguished from each other palynologically. The shape and extent of apertures was highly variable, some grains appeared inaperturate but the majority could be classified as either irregular or spiral. The irregular category was applied to grains with cracks or breaks. In some species furrow divided the surface of the grain into plate-like areas. Other aperturate types were 6-pantocolpate in *Ranzania* and tricolpate in all the remaining genera. Further pollen of both genera had an amorphous ektexine not organised in tectum columella and foot layer. Scattered small cavities were also visible in L.M. These channels or cavities were fibrous or granular as seen under TEM.

Blackmore and Heath (1984) stated that *B. vulgaris* had a perfect spiral aperture in less than 5% of the grains of each specimen and a more common type of grain had a single aperture which divided the grain into two equal interlocking parts and *Mahonia aquifolium* had pollen with irregularly syncolpate furrow-like apertures which divided the exine into 4-8 rounded or angular plates.

Spiraperturate pollen has now been described from a total of nine angiosperm families viz., Ranunculaceae, Berberidaceae, Scrophulariaceae, Acanthaceae, Eriocaulaceae, Costaceae, Liliaceae, Iridaceae and Xanthorrhoeaceae (Furness 1985).

The present study has shown that within the genus *Berberis* a range of pollen types are exhibited from inaperturate (*B. replicata, B. macrosepala*), 3-4 panto-polycolpate to spiroid and spiraperturate forms with irregular or perfect spiral. However, varying degrees of intergrading occurs in a few cases.

CONCLUSION

The pollen wall bears morphological characters with unique stable combinations embodying definite morphological entity of taxonomic and phylogenetic value. The genus *Berberis* is

4. Size and Shape

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Erdtman, G. 1960. The acetolysis method. A revised description. Svensk. Bot. Tidskr. 54 : 561-564.

Erdtman, G., 1952. Pollen Morphology and Plant Taxonomy. Angiosperms. Almqvist and Wiksell, Stockholm.

Furness, C.A. 1985. A review of spiraperturate pollen. Pollen et spores XXVII (3-4) : 307-320.

Kumazawa, M. 1936. Pollen grain morphology in Ranunculaceae, Lardizabalaceae and Berberidaceae. Jap. J. Bot. 8(1) : 19-46.

Nair, P.K.K. 1965a. Pollen grains of Western Himalayan Plants Asia Monographs, India 1(5) : 1-102.

Nair, P.K.K. 1965b. Trends in the morphological evolution of pollen and spores. J. Ind. Bot. Soc. 44 : 468-478.

Nair, P.K.K., 1970. Pollen Morphology of Angiosperms - A historical and phylogenetic study. Vikas Publ. House, Delhi.

Nair, P.K.K., 1979. The Palynological basis for the Triphyletic theory of angiosperms Grana : 141-144.

Nair, P.K.K., 1987-88. Morphological evolution of spores and pollen - An assay. J. Palynology 23-24 : 1-5 (G. Thanikaimoni Memorial volume)

Nowicke, J.W. and J.J. Skvaria, 1981. Pollen Morphology and Phylogenetic Relationships of the Berberidaceae. Smithsonian Contributions to Botany No. 50 : 1-83.

Rao, R.R., Husain, T. and Datt, B. 1994. Taxonomy of Indian Berberidaceae : Prospects and Problems J. Econ. Tax. Bot. 18(2) : 379-386.

Roland-Heydacker, F. 1974. Characters ultrastructuraux etcytochemiques particuliars du sporoderme des pollens de *Berberis vulgaris* L., et de *Mahonia aquifolium* Nutt. Compttes Rendes Academic des Sciences (Paris), 278 (D) : 1475-1477.

Stracker, H. 1963. Uber die magliche phylogenestische Bedeutung der Pollenmorphologie der madagassischen Bubbia perrieri R. Cap (Winteraceae) Grana Palynologica 4 : 355-360.

Walker, J.W. and J.A. Doyle, 1975. The basis of Angiosperm Phylogeny : Palynology. Ann. Missouri Bot. Gard. 62 : 664-723.

Walker, J.W. 1975. Comparative pollen morphology and phylogeny of the ranalean complex. In C.B. Beck (editor), Origin and Early Evolution of Angiosperms. Columbia Univ. Press, New York.

Wilson, T.K. 1964. Comparative morphology of the Canellaceae. III Pollen. Bot. Gaz., (Crawfordsville). 125 : 192-197.